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Molecular phylogeny of the superfamily Palaemonoidea (Crustacea : Decapoda : Caridea) based on mitochondrial and nuclear DNA reveals discrepancies with the current classification

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Abstract. Palaemonoidea is one of the most speciose superfamilies of Caridea. Since it was established, several classification schemes of Palaemonoidea have been proposed and modified. However, the current classification of Palaemonoidea is still in dispute. In this study, one mitochondrial gene (16S rRNA) and three nuclear genes (histone 3, 18S rRNA and 28S rRNA) were used to explore the phylogenetic relationships among the subgroups of the superfamily Palaemonoidea, including seven families with 25 affiliated genera. Based on the combined data with both maximum likelihood and Bayesian inference analyses, the results support the monophyly of Anchistioididae and Hymenoceridae. In contrast, Gnathophyllidae is suggested to be paraphyletic and Palaemonidae is shown to be a polyphyletic group. Our analyses reveal that the subfamily Palaemoninae could be approximately divided into three clades, and the branchiostegal groove is the probable morphological evidence of the environmental transition from sea to fresh water. Besides, for some of the Palaemonoidea families, their taxonomic status is obscure. A revision of Palaemonoidea and a re-evaluation of its constituent taxa appear to be necessary even though the systematic status of the subfamily Pontoniinae is still undetermined.

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Introduction

Palaemonoidea Rafinesque, 1815 is one of the most speciose superfamilies of Caridea, including more than 970 extant species in the world (De Grave and Fransen 2011). Palaemonoidean shrimps are distributed worldwide, in marine, brackish and freshwater habitats. They mainly inhabit streams, lakes, shallow sea and coast, but a few pontoniine species occur in the deep sea below 1820 m, and other taxa are found in groundwater (Li *et al*. 2007). According to De Grave *et al*. (2009), Palaemonoidea contains eight families, namely, Anchistioididae Borradaile, 1915, Desmocarididae Borradaile, 1915, Euryrhynchidae Holthuis, 1950, Gnathophyllidae Dana, 1852, Hymenoceridae Ortmann, 1890, Kakaducarididae Bruce, 1993, Palaemonidae Rafinesque, 1815 and Typhlocarididae Annandale & Kemp, 1913, following mainly the classification scheme of Martin and Davis (2001).

However, the current classification of the superfamily is largely based on the morphological characteristics of pereiopods, mouthparts and endopods, as proposed by Chace (1992) and Holthuis (1993). The scheme may not accurately reflect the phylogenetic relationships and the systematic status of these families within Palaemonoidea. Chace (1992), Chace and Bruce (1993) and Holthuis (1993) recognised only six families within Palaemonoidea. In the subsequent classification scheme of Martin and Davis (2001), Palaemonoidea consisted of eight families, with two subfamilies, Euryrhynchinae Holthuis, 1950 and Kakaducaridinae Bruce, 1993, elevated to familial rank. However, recent research based on molecular evidence questioned the familial status of Kakaducarididae, suggesting it is nested within the Palaemonidae (Page *et al*. 2008). Recently, Short *et al*. (2013) fully revised this family based on morphological characters and the former molecular study results. The revision concluded that the Kakaducarididae should be synonymised with the Palaemonidae, leaving only seven families within Palaemonoidea. Furthermore, the close relationship between Gnathophyllidae, Hymenoceridae and Pontoniinae gained more support through recent molecular analyses (Mitsuhashi *et al*. 2007; Bracken *et al*. 2009*a*; Li *et al*. 2011), challenging the current classification. In addition to the above controversies, the systematic status of

Anchistioididae and its relationship with Palaemonidae have not yet been completely resolved. Not to mention the most diverse and complicated pontoniine groups, these unresolved issues indicate that deeper phylogenetic research of the superfamily Palaemonoidea is essential and a full revision is needed.

So far, the traditional taxonomy (Chace 1992; Bruce 1993; Holthuis 1993), or the cladistic classification (Christoffersen 1990), of Palaemonoidea has been mainly based on morphological characters. Except for some taxa with economic value (e.g. *Macrobrachium* Bate, 1868; *Palaemon* Weber, 1795), the molecular systematics has been poorly studied. At familial level, only the systematic positions of several species-poor families such as Gnathophyllidae, Hymenoceridae (Mitsuhashi *et al*. 2007) and Kakaducarididae (Page *et al*. 2008) have been explored. At subfamilial level, Ashelby *et al*.'s (2012) probe into the systematic relationships in Palaemoninae primarily focused on the genera *Palaemon* and *Palaemonetes*, and Kou *et al*. (2013) preliminarily discussed the phylogenetic relationships among some Pontoniinae genera. However, in these preliminary studies a large number of palaemonoid taxa have been omitted, especially in Pontoniinae. Besides, in most works discussing the phylogeny of Decapoda or Caridea, the superfamily Palaemonoidea was only briefly mentioned (Porter *et al*. 2005; Tsang *et al*. 2008; Bracken *et al*. 2009*b*, 2010; Chan *et al*. 2010; Li *et al*. 2011). Therefore, the present study aims to construct the phylogenetic trees of Palaemonoidea using both mitochondrial (16S rRNA) and nuclear genes (histone 3, 18S rRNA, 28S rRNA). We attempt to explore the systematic relationships among these affiliated families of Palaemonoidea and provide new insights into the classification of this controversial superfamily.

Materials and methods

Taxon selection

In total, 44 palaemonoidean species from all seven families, 25 genera, plus two outgroup species, *Lysmata debelius* Bruce, 1983 and *Atyoida bisulcata* Randall, 1840, were included in this study. The classification of the 46 selected species followed De Grave and Fransen (2011), and the details of all the specimens are listed in Table 1. New sequences are marked by accession numbers in bold, while the remaining sequences were obtained from GenBank. All the specimens were identified before being preserved in 75–100% alcohol for DNA analysis.

DNA extraction and PCR amplification

The abdomen muscle, pleopod or eggs (5–20 mg) of the specimens were used for DNA extraction using a QIAamp DNA Mini Kit (Qiagen, Valencia, CA, USA). The DNA was eluted in 100 µL of sterile distilled H_2O (RNase free), and stored in −20°C freezer. The extracted DNA was checked by 1.5% agarose gel electrophoresis and ethidium bromide staining.

Partial segments of 16S rRNA (~450 bp) and three nuclear genes – histone 3 (~330 bp), 18S rRNA (~1800 bp) and 28S rRNA (~1000 bp) – were amplified by polymerase chain reaction (PCR). Polymerase chain reaction amplifications were performed in a 40 µL reaction, which contained 32–29 µL sterile distilled H_2O, 4 µL of 10 × PCR buffer (Mg^{2+} plus, Takara), 0.8 µL of dNTP (10 mM each), 0.8 µL of each primer (10 µM), 0.4 µL of Taq polymerase (5 unit μL^{-1}, Takara), and 1–4 µL of DNA extract.

The gene segments of 16S rRNA were amplified using the primers 16S-A/B (Wowor *et al*. 2009), with the following program: initial denaturation for 10 min at 94°C, followed by 30 to 40 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 40 s, extension at 72°C for 1 min, and a final extension at 72°C for 10 min. For the amplification of histone 3, the primers AF–AR (Colgan *et al*. 1998) were used, and the thermal cycle used was similar to that above except the annealing temperature was changed to 53°C. The 18S rRNA and 28S rRNA segments were amplified with the primers 18S-A/B (Medlin *et al*. 1988) and 28S-rD3.3f/28S-rD5b (Toon *et al*. 2009), respectively. The thermal cycling used was similar to that used for amplifying 16S rRNA segments except that the extension time was increased from 40 s to 1 min 30 s.

DNA sequencing

Polymerase chain reaction products were purified using the QIAquick Gel extraction Kit (Qiagen) before sequencing. The purified PCR products were bidirectionally sequenced with ABI 3730xl DNA Analyzer (Applied Biosystems, Foster City, CA, USA). The gene segments of 16S rRNA, histone 3 and 28S rRNA were sequenced using the same forward and reverse primers for PCR amplification. To sequence the 18S rRNA gene segment, 18S-A/B and 18S-W (this study: 5′-TAGCGTATATTAAAGTT GTT-3′) were used. The sequence chromatograms were checked using Chromas 2.23 (Technelysium Pty Ltd, available from http://technelysium.com.au/) by eye.

Phylogenetic analysis

Prior to analysing, forward and reverse sequence fragments were assembled and confirmed by ContigExpress (a component of Vector NTI Suite 6.0, Life Technologies, available from: http://zh.invitrogen.com/site/cn/zh/home/Products-and-Services/Applications/Cloning/vector-nti-software/vector-nti-advance software/vector-nti-advance-downloads/vector-nti-advance-archive.html). Then all the assembled sequences were aligned using MUSCLE 3.8 (Edgar 2004). We used GBlocks 0.91b (Castresana 2000) to eliminate the poorly aligned positions and the hyper-variable regions of the 16S, 18S and 28S rRNA datasets. GBlocks parameters optimised for datasets are listed in Table 2. For each dataset and the combined dataset, phylogenetic trees were constructed using maximum likelihood (ML) analysis with PhyML 3.0 (Guindon *et al*. 2010) performed on the ATGC bioinformatics platform and Bayesian inference (BI) analysis with MrBayes 3.2 (Huelsenbeck and Ronquist 2001). The best-fit models of DNA substitution for ML and BI analysis were selected by ModelTest 3.7 (Posada and Crandall 1998).

For ML, the analysis used the best-fit model for the combined dataset determined by ModelTest 3.7 (Posada and Crandall 1998). The confidence level at each branch was estimated by 1000 bootstrap replicates (BP). For BI analysis, the combined dataset was partitioned and analysed according to the optimum models selected from individual datasets. The Markov chains were run for 10 000 000 generations, with sampling every 1000 generations. After the first 25%, trees were discarded as burn-in,

Table 1. Details of the specimens and GenBank accession numbers in this study

'N/A' indicates unobtainable sequence data and new sequences are marked in bold. The abbreviations used in this table are: 16S, 16S rRNA; H 3, histone 3; 18S, 18S rRNA; 28S, 28S rRNA.

Family/subfamily	Species	Sampling locality	Voucher ID	GenBank accession number				Reference
				16S	H 3	18S	28S	
Anchistioididae	*Anchistioides* sp.	Okinawa, Japan	J2009-O	**KC515030**	**KC515074**	DQ642857	EF540849	Mitsuhashi *et al.* (2007)
	Anchistioides antiguensis	Caribbean	KC3051	EU920911	EU921043	EU920936	EU920971	Toon *et al.* (2009)
Desmocarididae	*Desmocaris* sp.	Unknown	ULLZ 8358	EU868651	N/A	EU868742	N/A	Bracken *et al.* (2009*a*)
Euryrhynchidae	*Euryrhynchus wrzesniowskii*	French Guyana	ULLZ 9070	EU868654	N/A	EU868745	N/A	Bracken *et al.* (2009*a*)
Gnathophyllidae	*Gnathophyllum americanum*	Okinawa, Japan	J2009-GA	**KC515031**	**KC515075**	DQ642848	EF540838	Mitsuhashi *et al.* (2007)
	Gnathophylloides mineri	Mexico	ULLZ 8596	EU868658	N/A	EU868749	N/A	Bracken *et al.* (2009*a*)
Hymenoceridae	*Phyllognathia ceratophthalma*	Panglao, Philippines	P2004-A	**KC515032**	**KC515076**	DQ642847	EF540840	Mitsuhashi *et al.* (2007)
	Hymenocera picta	Aquarium, Philippines	NSMT-Cr	DQ642881	JF346317	DQ642855	EF540839	Li *et al.* (2011) Mitsuhashi *et al.* (2007)
Palaemonidae								
Palaemoninae	*Arachnochium mirabile*	Mekong, Vietnam	V2010-D	**KC515033**	**KC515077**	**KC515052**	**KC515063**	
	Brachycarpus biunguiculatus	Kume, Japan	J2010-O	**KC515034**	**KC515078**	EU868778	**KC515064**	Bracken *et al.* (2009*a*)
	Coutierella tonkinensis	Hong Kong	H1991-B/KC3068	**KC515035**	EU921053	EU920937	EU920975	Toon *et al.* (2009)
	Creaseria morleyi	Americas	MLP102.1	DQ079710	DQ079671	DQ079746	DQ079784	Porter *et al.* (2005)
	Cryphiops caementarius	Americas	JC1219	DQ079711	DQ079672	DQ079747	DQ079785	Porter *et al.* (2005)
	Exopalaemon orientis	Xiamen, China	C2011-EORI/ OUMNH-ZC 2010–02–0078	**KC515036**	JN674387	**KC515053**	**KC515065**	Ashelby *et al.* (2012)
	Exopalaemon vietnamicus	Kuching, Malaysia	M2009-K	**KC515037**	**KC515079**	**KC515054**	**KC515066**	
	Leander sp.	Keelung, Taiwan	T2007-F	**KC515038**	**KC515080**	N/A	N/A	
	Leander tenuicornis	Vaca Key, USA	ULLZ7765/OUMNH-ZC 2009–05–0004	JN674327	JN674388	EU868783	N/A	Ashelby *et al.* (2012) Bracken *et al.* (2009*a*)
	Leandrites deschampsi	Singapore	S2011-LD	**KC515039**	**KC515081**	N/A	**KC515067**	
	Leptocarpus potamiscus	Sungai Petani River, Malaysia	OUMNH-ZC 2009–03–0006	JN674328	JN674392	N/A	N/A	Ashelby *et al.* (2012)
	Leptopalaemon gagadjui	Australia	GUL10_8	EF588304	EU249459	EF588298	EF588302	Page *et al.* (2008)
	Leptopalaemon glabra	Australia	GUK6_2	EF588318	EU249461	EU249463	EU249464	Page *et al.* (2008)
	Macrobrachium nipponense	Qingdao, China	C2010-M2	**KC515040**	**KC515082**	DQ531769	**KC515068**	Yu (2006)
	Macrobrachium pilimanus	Unknown	KC3110	GQ487497	GQ487524	GQ487505	GQ487513	Bracken *et al.* (2010)
	Macrobrachium potiuna	Unknown	KC2094	DQ079721	DQ079685	DQ079756	DQ079797	Porter *et al.* (2005)
	Macrobrachium rosenbergii	Timika, Irian Jaya	MSLKHC-Maros	DQ642882	JF346320	DQ642856	EF540848	Li *et al.* (2011) Mitsuhashi *et al.* (2007)
	Macrobrachium superbum	Xiamen, China	C2011-MS	**KC515041**	**KC515083**	**KC515055**	**KC515069**	
	Nematopalaemon tenuipes	Yunlin, Taiwan	T2009-B	**KC515042**	**KC515084**	N/A	N/A	
	Palaemon concinnus	Hainan, China	C2011-PCON	**KC515043**	**KC515085**	**KC515056**	**KC515070**	
	Palaemon debilis	Hainan, China	C2011-PD	**KC515044**	**KC515086**	**KC515057**	**KC515071**	
	Palaemon elegans	The Fleet, England	KACpael	DQ079729	DQ079696	DQ079764	DQ079807	Porter *et al.* (2005)
	Palaemon gravieri	Yellow Sea, China	C2011-PG	**KC515045**	**KC515087**	**KC515058**	N/A	
	Palaemon macrodactylus	Tokyo Bay, Japan	OUMNH-ZC 2001–09–0053	DQ642875	JN674385	DQ642849	EF540847	Ashelby *et al.* (2012) Mitsuhashi *et al.* (2007)
	Palaemon pacificus	Hainan, China	C2011-PPAC	**KC515046**	**KC515088**	**KC515059**	**KC515072**	
	Palaemon serenus	Moreton Bay, Australia	A2005-PS	**KC515047**	**KC515089**	AY374179	**KC515073**	

(*continued next page*)

Table 1. (*continued*)

Family/subfamily	Species	Sampling locality	Voucher ID	GenBank accession number 16S	H 3	18S	28S	Reference
	Palaemon serrifer	Qingdao, China	C2010-P2/MACR052	**KC515048**	**KC515090**	**KC515060**	FM955538	Wowor *et al.* (2009)
	Palaemonetes atrinubes	Australia	OUMNH-ZC 2009–21–0012	JN674352	JN674399	AY374178	AY374150	Ashelby *et al.* (2012)
	Palaemonetes paludosus	Jefferson County, USA	MLP124	N/A	DQ079684	DQ079755	DQ079796	Porter *et al.* (2005)
	Palaemonetes pugio	Ocean Springs, USA	ULLZ7458/OUMNH-ZC 2009–07–0005	JN674355	JN674371	EU868791	N/A	Ashelby *et al.* (2012) Bracken *et al.* (2009*a*)
	Palaemonetes vulgaris	Ocean Springs, USA	OUMNH-ZC 2009–07–0006	JN674358	JN674372	AY743941	AY739184	Ashelby *et al.* (2012) Babbitt and Patel (2005)
	Urocaridella antonbruunii	Okinawa, Japan	J2000-M52	**KC515049**	**KC515091**	**KC515061**	N/A	
	Urocaridella pulchella	Okinawa, Japan	J2009-UPU	**KC515050**	**KC515092**	**KC515062**	N/A	
Pontoniinae	*Conchodytes meleagrinae*	Okinawa, Japan	J2000-M36	**KC515051**	**KC515093**	EF540837	EF540842	Mitsuhashi *et al.* (2007)
	Dactylonia sp.	Panglao, Philippines	T2010-D	DQ642876	**KC515094**	DQ642850	EF540841	Mitsuhashi *et al.* (2007)
Typhlocarididae	*Typhlocaris salentina*	Unknown	ULLZ 9152	EU868713	N/A	EU868808	N/A	Bracken *et al.* (2009*a*)
Atyoidae	*Atyoida bisulcata*	Unknown	KC2138	DQ079704	DQ079661	DQ079738	DQ079774	Porter *et al.* (2005)
Hippolytidae	*Lysmata debelius*	Unknown	MLP121	DQ079718	DQ079681	DQ079752	DQ079793	Porter *et al.* (2005)

the remaining trees were used to construct the 50% majority rule consensus tree and estimate posterior probabilities (PP). The phylogenetic parameters were diagnosed by Tracer 1.4 (Rambaut and Drummond 2007) to make sure convergence was reached.

Alternative phylogenetic hypotheses were statistically tested using the Kishino–Hasegawa (KH) test (Kishino and Hasegawa 1989) in Tree-Puzzle 5.2 (Schmidt *et al*. 2002) and using approximately unbiased (AU) test (Shimodaira 2002) in CONSEL (Shimodaira and Hasegawa 1999). The null hypothesis for all topology testing is that there is no difference between trees.

Results

Sequences

Including the GenBank sequences, we analysed 45 16S rRNA sequences, 43 histone 3 sequences, 43 18S rRNA sequences and 34 28S rRNA sequences in all. The combined aligned dataset consisted of 2614 bp (~70.2% of the original 3723 bp alignment) after the poorly aligned positions and the hyper-variable regions were removed with Gblocks. The alignment gaps were represented as '-' and the missing data were designated as '?' in the analyses. In some cases, the substitution model of some partitions selected by ModelTest was not available in MrBayes, and we used the most approximate model available instead. The characteristics of the four individual and the combined datasets, their empirical base frequencies, rate matrix, gamma shape parameter, proportion of invariable sites, the substitution models selected by ModelTest and the models implemented in MrBayes are listed in Table 3.

Phylogenetic analyses

The tree topologies derived from the ML and BI analyses were highly congruent, except for the position of the genus *Nematopalaemon* Holthuis, 1950 and a few internal nodes. Both ML and BI trees are presented for comparison of the different topologies (Figs 1, 2).

At the familial level, the family Typhlocarididae locates in the basal position of the tree in both analyses with moderate support (PP = 0.96, BP = 77%). The clustering of Desmocarididae and Euryrhynchidae is strongly supported by the analyses (PP = 1.00, BP = 100%), suggesting a close relationship between these two families. The family Palaemonidae could not form a single clade in the tree and the monophyly of Palaemonidae was also rejected by the AU and KH tests ($P < 0.001$, for both). In contrast to the polyphyly of Palaemonidae, our results support the monophyly of Anchistioididae (PP = 1.00, BP = 97%) and Hymenoceridae (PP = 1.00, BP = 100%). However, the taxonomic status of these two families is obscure. The family Anchistioididae appears to be sister to the marine Palaemoninae taxa. By comparison, Hymenoceridae and Gnathophyllidae constitute a clade with high support (PP = 0.99, BP = 99%), with the latter forming a paraphyletic assemblage.

The two Pontoniinae genera *Conchodytes* and *Dactylonia* cluster together and show a high affinity to Hymenoceridae and Gnathophyllidae. These three groups form a clade with high support (PP = 1.00, BP = 99%). The monophyly of the subfamily Palaemoninae was rejected by the AU and KH tests

Table 2. GBlocks parameters optimised for the dataset. The abbreviations used in this table are: 16S, 16S rRNA; 18S, 18S rRNA; 28S, 28S rRNA.

Gene	Number of sequences	Minimum number of sequences for a conserved position	Minimum number of sequences for a flanking position	Maximum number of contiguous non-conserved positions	Minimum length of a block	Allowed gap positions
16S	45	25	39	8	5	With half
18S	43	24	34	8	5	With half
28S	34	19	32	8	5	With half

Table 3. The information of different datasets and the substitution model selected by ModelTest

The abbreviations used in this table are: 16S, 16S rRNA; H 3, histone 3; 18S, 18S rRNA; 28S, 28S rRNA; Rmat, Rate matrix.

Dataset	Number of sites	Base frequencies (A, C, G, T)	Rmat	Gamma shape parameter	Proportion of invariable sites	Model selected by ModelTest	Model implemented in MrBayes
16S	374	0.3372, 0.0713, 0.1874, 0.4040	0.9907, 5.8183 1.0701, 0.5092 11.3370, 1.0000	0.4760	0.3202	TrN+I+G	GTR+I+G
H3	269	0.2049, 0.2769, 0.2853, 0.2329	1.0000, 3.2338 1.0000, 1.0000 4.9686, 1.0000	1.1856	0.6282	TrN+I+G	GTR+I+G
18S	1768	0.2510, 0.2301, 0.2764, 0.2424	0.5028, 1.0960 0.8499, 0.9555 2.3722, 1.0000	0.6167	0.6683	GTR+I+G	GTR+I+G
28S	203	0.1614, 0.2263, 0.3869, 0.2255	1.0000, 1.7272 1.0000, 1.0000 3.4098, 1.0000	0.6945	0	GTR+G	GTR+G
Combined	2614	0.2417, 0.2142, 0.2790, 0.2650	0.4279, 2.2608 1.4712, 0.8807 2.7131, 1.0000	0.5462	0.5671	GTR+I+G	GTR+I+G

($P < 0.05$, for both). In our tree, Palaemoninae could be divided into at least three major clades, referred as clade I, II and III. Within clade I, *Leander* is a sister group to *Urocaridella* (PP = 1.00, BP = 100%), and both genera are strongly supported as monophyletic (PP = 1.00, BP = 100%, for both). Clade II includes the species of *Coutierella*, *Exopalaemon*, *Palaemon* and *Palaemonetes*. The latter two genera are indicated to be polyphyletic, while two *Exopalaemon* species form a monophyletic group (PP = 1.00, BP = 100%) closely related to some of the *Palaemon* species. Clade III consists of seven Palaemoninae genera, namely, *Arachnochium*, *Creaseria*, *Cryphiops*, *Leandrites*, *Leptocarpus*, *Leptopalaemon* and *Macrobrachium*. The genus *Macrobrachium* is suggested to be paraphyletic and two species cluster with *Arachnochium* (PP = 1.00, BP = 98%).

Discussion

Superfamily Palaemonoidea

In this study, the atyid species *Atyoida bisulcata* clusters with the hippolytid species *Lysmata debelius* as the root of the phylogenetic trees. The remaining 44 palaemonoid species are grouped together and form a well-supported clade in our analyses. However, several Palaemonoidea families could not form a monophyletic group and some families' taxonomic status seems to be invalid according to the present phylogenetic analyses.

The marine family Anchistioididae, which includes only one genus, *Anchistioides* Paul'son, 1875, was once considered a genus of Pontoniinae Kingsley, 1878 (Gordon 1935). This viewpoint was challenged by Gurney (1938) based on some larval morphological characteristics of *Anchistioides* (e.g. the presence of the pterygostomial spine, the very large posterior branchiostegal spine and the dorsal spine on the third abdominal somite) and this genus was elevated to a subfamily of Palaemonidae. Later, Chace (1992) resurrected Anchistioididae Borradaile, 1915, separated from Palaemonidae. The separation was supported in the subsequent schemes (Bruce 1993; Chace and Bruce 1993; Holthuis 1993; Martin and Davis 2001; De Grave *et al*. 2009). However, Mitsuhashi *et al*. (2007) indicated a close relationship between Anchistioididae and Palaemonidae from 18S rRNA and 28S rRNA combined data analysis. Bracken *et al*. (2009*a*) obtained a similar result in their investigation on the phylogenetic relationships within the infraorder Caridea, but further discussion about this issue was lacking. In the present phylogenetic analyses the two anchistioidid species cluster with several marine palaemonine genera, so the familial status of Anchistioididae is not well supported in the current analysis. However, in view of the special mouthpart characteristics of Anchistioididae, a comparison of the larval morphology of Anchistioididae and these marine palaemonine species would be necessary for a definite conclusion to be reached (Mitsuhashi *et al*. 2007).

Another two marine families, Gnathophyllidae and Hymenoceridae, which were previously treated as a single family of Gnathophyllidae under Palaemonoidea (Holthuis 1955), were separated from each other on the morphological differences of the third maxilliped by Chace (1992). However, Bruce (1986, 1988) and Yang and Ko (2002, 2004) reported that the larvae of Gnathophyllidae and Hymenoceridae are similar to those of some pontoniine species and both Mitsuhashi *et al*. (2007) and Bracken *et al*. (2009*a*) indicated the close

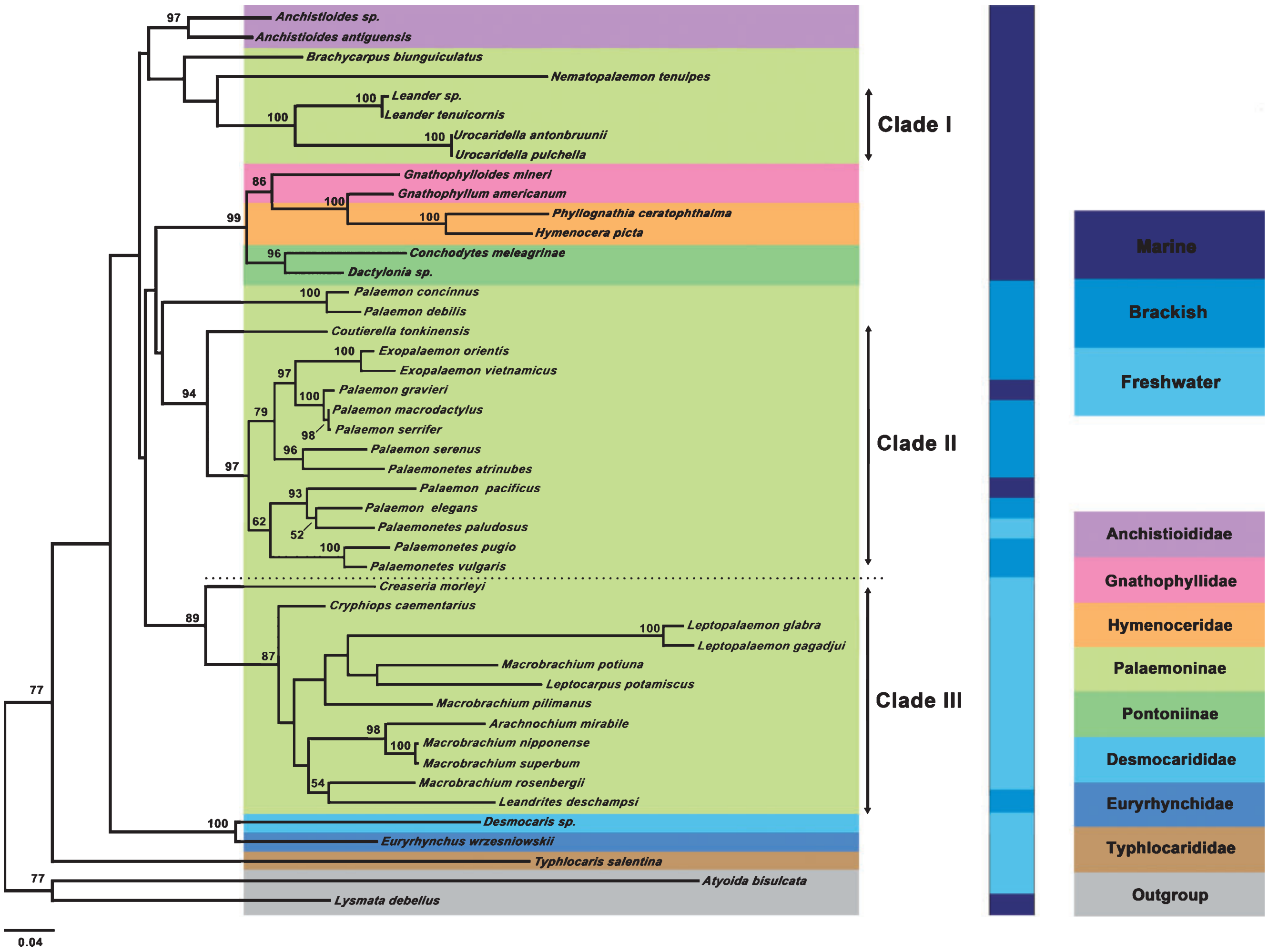

Fig. 1. Phylogenetic tree obtained by maximum likelihood analysis of DNA sequences based on the combined dataset. The percentages of the maximum likelihood bootstrap values are indicated on each branch. The values under 50% are not shown. The species of each family are marked by different background colours. The water environments inhabited by the studied species are indicated by the vertical bars behind branches. The colour references of the background colours and the vertical bars are interpreted in the figure legend.

relationship between them. In this study, *Gnathophyllum* Latreille, 1819, *Gnathophylloides* Schmitt, 1933, *Hymenocera* Latreille, 1819 and *Phyllognathia* Borradaile, 1915, plus two Pontoniinae genera, *Conchodytes* Peters, 1852 and *Dactylonia* Fransen, 2002, were included. Tallied with the former studies, our results support the family Gnathophyllidae as a paraphyletic group. Additionally, Gnathophyllidae and Hymenoceridae form a clade with high support with two Pontoniinae genera in our tree, reflecting a close relationship among them.

The troglobitic freshwater family Typhlocarididae, which has only been found in the subterranean waters in the Mediterranean area, includes four species in one genus, *Typhlocaris* Calman, 1909 (Holthuis 1986; Froglia and Ungaro 2001; Tsurnamal 2008). Annandale and Kemp (1913) erected the subfamily Typhlocaridinae under Palaemonidae, and Chace (1992) elevated it to familial level, incorporating another palaemonid subfamily Euryrhynchinae based on the similarity of their mouthparts. Nevertheless, the proposal was not widely accepted in subsequent schemes (Martin and Davis 2001; De Grave *et al*. 2009). In our tree, Typhlocarididae always locates in the most basal position of the whole palaemonoid clade and does not group with Euryrhynchidae, which is consistent with Bracken *et al*. (2009*a*). The extremely peculiar morphological characteristic combination of paired, complete post-antennal suture, degenerative eyes and the absence of antennal spine suggest the family is a unique taxon of Palaemonoidea, and a close relationship between Euryrhynchidae and Typhlocarididae seems untenable. Instead, Euryrhynchidae and Desmocarididae are sister groups in the present analyses. These two species-poor freshwater families share some similar morphological features, e.g. the structure of the mandible, the structure of the antennular peduncle, the presence of asetal brush on the fifth pereiopod and cuspidate setae on their appendix masculine (De Grave 2007; Bracken *et al*. 2009*a*). In addition, Euryrhynchinae is only known from South America and west Africa, while Desmocarididae is endemic to west and central African (Powell 1976, 1977). This geographical distribution probably suggests that these two

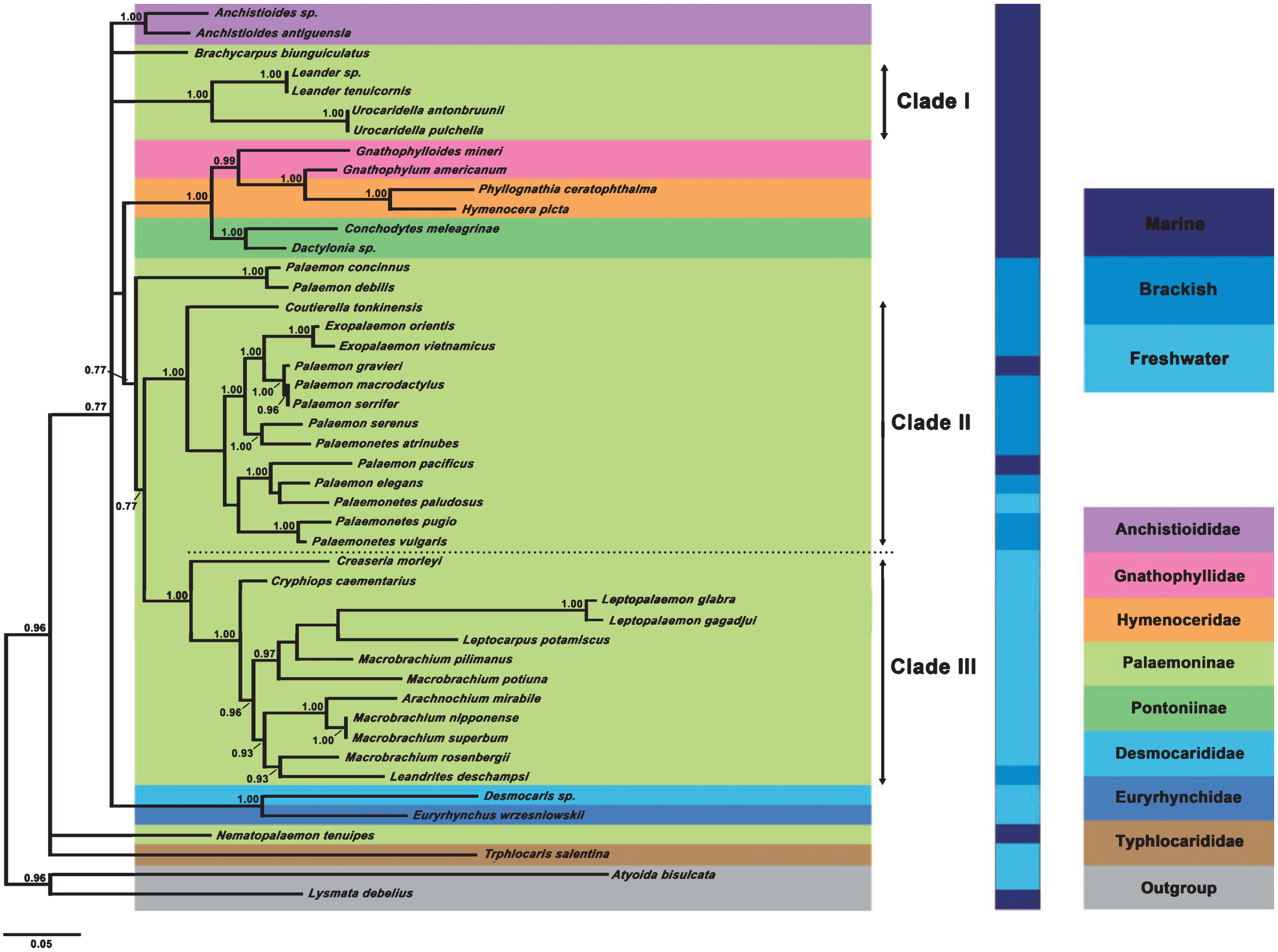

Fig. 2. Phylogenetic tree obtained by Bayesian inference analysis of DNA sequences based on the combined dataset. Bayesian posterior probabilities are indicated on each branch. The values under 0.75 are not shown. The species of each family are marked by different background colours. The water environments inhabited by the studied species are indicated by the vertical bars behind branches. The colour references of the background colours and the vertical bars are interpreted in the figure legend.

families share a common ancestor, which originated in Gondwanaland.

Subfamily Palaemoninae

Our molecular analyses demonstrate the family Palaemonidae as a polyphyletic assemblage. On account of the enormous diversity in morphology, lifestyle and habitat, the assessment of the systematic position and relationship of the subfamily Pontoniinae is arduous, and is not the focus of this study. In fact, we have started the molecular phylogenetic analysis of this subfamily (Huang 2012; Kou *et al.* 2013). Regardless of Pontoniinae, the 15 studied genera of the subfamily Palaemoninae could be divided into three major clades in the current analyses.

The first major clade (clade I) consists of two marine palaemonine genera, namely, *Leander* Desmarest, 1849 and *Urocaridella* Borradaile, 1915, while another two marine species *Brachycarpus biunguiculatus* (Lucas, 1846) and *Nematopalaemon tenuipes* (Henderson, 1893) may also be affiliated with this clade, but with weak support (<50%) in the ML analysis.

Both *Leander* and *Urocaridella* are corroborated to be monophyletic in the current study. *Urocaridella* was previously considered to be a synonym of *Leander* by Holthuis (1950), as a monotypic genus with a single species *Urocaridella urocaridella* (Holthuis, 1950). However, Chace and Bruce (1993) re-established the genus *Urocaridella* mainly based on the shape of the rostrum and mandibular palp and consigned other species into this genus. Our analyses strongly support *Urocaridella* as a sister taxon to *Leander*. Both genera inhabit the shallow sea (Bruce 1967, 1991; Yokes and Galil 2006). Additionally, they share many common characters, e.g. the absence of branchiostegal groove, the posterior margin of the telson with a pair of median feathered setae, the last three pereiopods with simple dactyli and the first pleopod of male with appendix interna on endopod (Holthuis 1950, 1955; Chace and Bruce 1993).

In common with *Leander* and *Urocaridella*, *Brachycarpus* lacks a branchiostegal groove and has an appendix interna on the first pleopod of the male. However, *Brachycarpus* can be easily distinguished from the former two genera by the presence of hepatic spine and the absence of branchiostegal spine. On the other hand, *Brachycarpus* is somewhat similar to the anchistioidids in the well-developed and compressed toothed rostrum and the biunguiculate dactyli of the last three pereiopods as well as the absence of a branchiostegal groove (Holthuis 1950, 1951, 1952*a*; Okuno and Osawa 1994). Morphologically, Anchistioididae correlates with Palaemoninae in some respects (e.g. posterior margin of telson generally with two pairs of spines only; the presence of an appendix interna on the first pleopod of the male). These similar characteristics coupled with a marine habitat might suggest an affinity between *Brachycarpus* and the family Anchistioididae.

Nematopalaemon resembles the genus *Urocaridella* in the shape of the rostrum. Both have a long and slender rostrum with an elevated basal crest on the dorsal margin. *Nematopalaemon* also lacks a branchiostegal groove. However, according to Holthuis (1950), *Nematopalaemon* is markedly different from other palaemonine groups in its thread-like posterior pereiopods, which superficially resemble the species of the genus *Nematocarcinus* A. Milne-Edwards, 1881 (Nematocarcinidae). In addition, unlike other marine palaemonine genera, the first pleopod of the male bears no appendix interna in *Nematopalaemon.* Such a combination of peculiar characters is unique in the whole superfamily Palaemonoidea. In consideration of the isolated position of *Nematopalaemon* in the BI tree, *Nematopalaemon* might have a relatively remote relationship to other palaemonine groups.

The second major clade (clade II) includes the species of four genera, *Coutierella* Sollaud, 1914, *Exopalaemon* Holthuis, 1950, *Palaemon* Weber, 1795 and *Palaemonetes* Heller, 1869. The species of these genera are usually distributed in a variety of water environments, from freshwater lakes and streams to brackish waters in littoral zones or estuaries, as well as completely marine habitat. In addition, a considerable portion of the species can tolerate a wide salinity range, living from almost fresh water to polyhaline water. Morphologically, they also share the common characters of the presence of branchiostegal groove and branchiostegal spine, the absence of hepatic spine and the first pleopod of male without appendix interna on endopod (Holthuis 1950; Bruce 1989; Chace and Bruce 1993).

Bruce (1989) resurrected the monotypic genus *Coutierella* (including the single species *C. tonkinensis* Sollaud, 1914 with two subspecies), which was treated as a synonym of *Palaemonetes* by Kemp (1925). In agreement with Bruce, our results support the separation. Morphologically, *Coutierella* could be easily distinguished from *Palaemonetes* by the telson armed with three or more pairs of posterior spines, the fourth thoracic segment lacking a well-developed pleurobranch, the presence of subspatulate chelae on the second pereiopods and the specialised mouthparts (Bruce 1989).

The Indo-West Pacific restricted genus *Exopalaemon* was erected by Holthuis (1950) as a subgenus of *Palaemon*. Subsequently, he elevated *Exopalaemon* to a full generic rank (Holthuis 1980), which was accepted by Chace and Bruce (1993). In the current analyses, two *Exopalaemon* species cluster together and form a monophyletic group. However, in agreement with Ashelby *et al*. (2012), its generic level status is questionable as both trees suggest *Exopalaemon* is nested within some species of *Palaemon*.

In contrast to the monophyly of *Exopalaemon*, the genus *Palaemonetes* is identified to be polyphyletic. According to Chace and Bruce (1993), *Palaemonetes* is distinguished from *Palaemon* only by the absence of a mandibular palp. However, due to the variation of the mandibular palp in different species or individuals, this character seems to be unreliable in classification (Fujino and Miyake 1968; Chace 1972; Bray 1976; Boulton and Knott 1984). Our result is consistent with those reported by Boulton and Knott (1984) and Murphy and Austin (2003), which support the very close relationship between *Palaemon* and *Palaemonetes*, especially the two Australian endemic species, *Palaemon serenus* Heller, 1862 and *Palaemonetes atrinubes* Bray, 1976. The status of *Palaemonetes* has been queried previously (Chace 1972; Bray 1976; Walker and Poore 2003; Ashelby *et al*. 2012), with the conclusion that *Palaemonetes* is likely to be the synonym of *Palaemon* with reservation. With the genetic evidence presented here, as well as the previous morphological and allozymic evidence (Boulton and Knott 1984), the proposal appears to be increasingly reasonable.

As in *Palaemonetes*, our results reject the monophyly of *Palaemon. Palaemon concinnus* Dana, 1852 and *Palaemon debilis* Dana, 1852 form a clade distant from the other *Palaemon* species. Both species have the same characters of rostrum with single dorsal teeth on carapace behind posterior orbital margin and carpus of the second pereiopod markedly longer than chela. In addition, they can tolerate freshwater environments (Chace and Bruce 1993). The other *Palaemon* species clustered with the *Palaemonetes* and *Exopalaemon* species, forming a mixed clade. However, a recent study indicated that deep geographical relationships may be concealed beneath this apparently miscellaneous assemblage (Ashelby *et al*. 2012). *Palaemon* used to be one of the most species-rich genera in the subfamily Palaemoninae; the number of species of this genus is only less than those of *Macrobrachium* in the subfamily. Even after many species were transferred out and some subgenera were elevated to generic level (e.g. *Exopalaemon*, *Nematopalaemon*), *Palaemon* still consists of more than 40 species (De Grave and Fransen 2011), and including *Palaemonetes* it reaches a total of more than 70 species. The great species number and diversity necessitates a reclassification of this assemblage. In our opinion, a comprehensive review of all the constituent species of *Palaemonetes* and *Palaemon* is essential, and a revision should be put on the agenda.

Five palaemonine genera principally living in fresh water (i.e. *Arachnochium* Wowor & Ng, 2010, *Creaseria* Holthuis, 1950, *Cryphiops* Dana, 1852, *Leptopalaemon* Bruce & Short, 1993 and *Macrobrachium* Bate, 1868) and two euryhaline genera that are encountered in fresh, brackish and salty waters (i.e. *Leandrites* Holthuis, 1950 and *Leptocarpus* Holthuis, 1950) comprise the third major clade (clade III).

Wowor and Ng (2010) established the genus *Arachnochium* for *Palaemon mirabilis* Kemp, 1917, which had been placed in *Macrobrachium* for a long time. Meanwhile, another species, *Macrobrachium kulsiense* Jayachandran, Lal Mohan & Raji, 2007, was also transferred into the genus *Arachnochium*. *Arachnochium* differs from *Macrobrachium* in the very slender and glabrous second pereiopod and some other features (Wowor and Ng 2010). However, our analyses suggest a very close relationship between *Arachnochium* and *Macrobrachium*, so the generic status of *Arachnochium* seems doubtful. According to Jayachandran *et al*. (2007) and Wowor and Ng (2010), *Arachnochium* resembles some species of *Macrobrachium* (e.g. *M. moorei* (Calman, 1899) and *M. patheinense* Phone & Suzuki, 2004). In view of the limited species coverage, it is suggested that the genus should be retained before an exhaustive examination.

Creaseria morleyi (Creaser, 1936) is one of the few palaemonine shrimps living in subterranean fresh waters, and is restricted to the submerged caves on the Yucatan Peninsula. According to Holthuis (1950), it is characterised by reduced eyes, the presence of a branchiostegal spine, the absence of a branchiostegal groove and a two-jointed mandibular palp. The present study rejects the close relationship between *Creaseria* and another troglobitic palaemonoid family, Typhlocarididae, proposed by Pereira (1997). Instead, our results support *Creaseria* clusters with *Cryphiops* and *Macrobrachium* as observed in previous molecular analyses (Porter *et al*. 2005; Page *et al*. 2008; Bracken *et al*. 2009*b*, 2010). *Creaseria* is the only extant freshwater palaemonid genus without a branchiostegal groove. Combined with its basal position in the clade, it is possible that *Creaseria* is a relict taxon of the primitive palaemonids invading freshwater from the sea.

Cryphiops Dana, 1852 consists of six freshwater species restricted to Central and South America (De Grave and Fransen 2011). *Cryphiops* is very similar to *Macrobrachium* except for the absence of the hepatic spine on the carapace (Holthuis 1952*a*, 1952*b*), which is considered to be an inadequate criterion by Short (2004). Our analyses identify the strong affinity between *Cryphiops* and *Macrobrachium* in accordance with both cladistic (Pereira 1997) and molecular analyses (Pereira *et al*. 2002; Porter *et al*. 2005; Page *et al*. 2008; Bracken *et al*. 2009*b*, 2010; Pileggi and Mantelatto 2010). It is very probable that *Cryphiops* is not a valid genus and is a synonym of *Macrobrachium*. However, owing to the limited species coverage in the present analyses, the monophyly of the genus *Cryphiops* is uncertain and a full revision is needed to make its taxonomic status conclusive.

Holthuis (1950) believed *Leptocarpus* is closely related to *Exopalaemon* and *Nematopalaemon*, mainly based on the parallel of rostrum and mouthparts. Pereira (1997) fully supported this view in his cladistic analysis. However, our analyses suggest *Leptocarpus* has a close relationship with *Macrobrachium*, which could be supported by their similar habitat. Besides, both *Leptocarpus* and *Macrobrachium* are somewhat alike in appearance, lacking branchiostegal spines while having a branchiostegal groove and a three-jointed mandibular palp. The only distinction is the presence of hepatic spines in the latter.

Bruce (1993) established the freshwater family Kakaducarididae according to the typical mouthpart morphology coupled with the form of the appendix masculine, which consists of only three monotypic genera (*Calathaemon* Bruce & Short, 1993, *Kakaducaris* Bruce, 1993 and *Leptopalaemon* Bruce & Short, 1993). However, the familial status of Kakaducarididae is doubtful according to the succedent studies (Page *et al*. 2008; Bracken *et al*. 2009*a*). Recently, Short *et al*. (2013) fully revised Kakaducarididae and reappraised its taxonomic status based on morphological characters and the molecular study results by Page *et al*. (2008). The revision concluded that the Kakaducarididae should be synonymised with the Palaemonidae, and the genus *Kakaducaris* is synonymised with *Leptopalaemon*. As a result, now only seven families remain within Palaemonoidea. The genus *Calathaemon*, which was provisionally included in the Kakaducarididae, is reassigned back to the Palaemonidae, and the genus *Leptopalaemon* will be included in the Palaemonidae as well. In the present study, two *Leptopalaemon* species were nested within the palaemonid clade (clade III) and closely related to the freshwater genus *Macrobrachium*, in agreement with recent results. This affinity is also reinforced by the high similarity in general morphology between *Leptopalaemon* and other palaemonid genera, except for the filtratory mouthparts and unique form of the appendix masculine (Page *et al*. 2008). Furthermore, *L. glabra* (previously belonging to genus *Kakaducaris*) and *L. gagadjui* were grouped together with strong support, which corroborates the classification of *Kakaducaris* synonymised with *Leptopalaemon* by Short *et al*. (2013).

As one of the most diverse and speciose genera of Caridea (243 species, see De Grave and Fransen 2011), the monophyly of *Macrobrachium* has been under suspicion for a long time. Moreover, this doubt has proven to be not groundless by recent phylogenetic studies (Pereira *et al*. 2002; Murphy and Austin 2002, 2003, 2005; Liu *et al*. 2007; Wowor *et al*. 2009; Pileggi and Mantelatto 2010). Not surprisingly, the *Macrobrachium* species in the present study fell in a clade intermingling with other genera in our tree, which supports the paraphyly of *Macrobrachium*. With considerable biogeographic, morphological and molecular evidence, the genus is ripe for a thorough rearrangement and reclassification in the near future.

Unexpectedly, *Leandrites deschampsi* (Nobili, 1903) shows close relationship with *Macrobrachium* in our analyses. According to Holthuis (1950), the genus *Leandrites* closely resembles *Leander*. Nevertheless, *Leandrites* could be distinguished from *Leander* by the absence of the mandible palp and the presence of a slender median process on the fourth thoracic sternite. Furthermore, all the *Leandrites* species are restricted to South-east Asia, while the *Leander* species spread throughout nearly all tropical and subtropical seas worldwide, especially *Leander tenuicornis* (Say, 1818) (Chace and Bruce 1993; Bruce 2002). In addition, *Leandrites deschampsi* inhabits brackish water in mangrove creeks (Johnson 1961, 1965), which is similar to some *Macrobrachium* species (e.g. *M. equidens* (Dana, 1852), *M. lar* (Fabricius, 1798)). Instead, *Leander* lives in the shallow sea, floating on weed or attaching to plants under water. In spite of this, more evidence is still needed to verify the great affinity between *Leandrites* and the freshwater palaemonids. After all, *Leandrites* has the characters of a lack of branchiostegal groove and the first pleopod of the male with appendix interna, which only appears in marine palaemonine genera (e.g. *Brachycarpus*, *Leander* and *Urocaridella*).

Some taxonomic characters in Palaemonoidea

Within the superfamily Palaemonoidea, the mandibular palp is absent in six families and only exists in the family Palaemonidae. For Palaemonidae, the mandibular palp is merely present in a few genera of Pontoniinae (i.e. *Exoclimenella*, *Eupontonia*, *Palaemonella* and *Vir*), which probably has plesiomorphic status in Pontoniinae shrimps (Kou *et al*. 2013). Counting *Calathaemon* and *Leptopalaemon*, even in Palaemoninae, the mandibular palp is present in 14 of the 23 extant genera, absent in eight genera and variable in one genus. Though the mandibular palp is an important diagnostic characteristic, it is probably inadequate as a classification criterion at the generic level. As discussed above, there is intraspecific variation in *Palaemon debilis* (Chace, 1972) and *Palaemonetes australis* Dakin, 1915 (Bray 1976). Besides, the palp also varies in the genus *Urocaridella*: well developed, two segments (*U. urocaridella* Holthuis, 1950); to vestigial (*U. vestigialis* Chace & Bruce, 1993); to fully absent (*U. antonbruunii* (Bruce, 1967)) (see Li *et al*. 2004). Furthermore, the number of segments of the mandibular palp varies in *Palaemon* interspecifically (Holthuis 1950) and intraspecifically (Fujino and Miyake 1968). Perhaps, just as Ashelby *et al*. (2012) presumed, the mandibular palp is more likely to be a homoplastic character in different taxa, as a structure for adapting to certain lifestyles or habitats.

Compared with the mandibular palp, the branchiostegal groove seems to be a more significant taxonomic character. The branchiostegal groove is missing in all the marine Palaemonoidea families (i.e. Anchistioididae, Gnathophyllidae and Hymenoceridae), all the genera of Palaemoninae restricted to marine habitats (i.e. *Brachycarpus*, *Leander* and *Urocaridella*) and all the Pontoniinae genera (all sea-living). On the contrary, it is present in almost all the freshwater palaemonoid shrimps, except in a few subterranean fauna, such as the Typhlocarididae genus *Typhlocaris* and the Palaemonidae genus *Creaseria.* As for those genera distributed across a wide salinity range of water habitats, their carapace is either with branchiostegal groove (in *Coutierella*, *Exopalaemon*, *Palaemon* and *Palaemonetes*) or without (in *Leandrites* and *Nematopalaemon*). Thus the variation pattern likely reflects the evolution of the branchiostegal groove accompanied by the invasion from marine to freshwater environments.

Conclusion

Our study using four different genes constructed the phylogenetic trees and inferred the general phylogenetic relationships of seven Palaemonoidea families with 25 affiliated genera. Typhlocarididae locates in the basal position of the tree. Desmocarididae and Euryrhynchidae are shown to be sister groups. Based on the limited taxonomic coverage, our analyses support the monophyly of Anchistioididae and Hymenoceridae. However, their familial statuses need reassessment. By comparison, Gnathophyllidae is suggested to be paraphyletic, while closely related to Hymenoceridae and Pontoniinae. The monophyly of Palaemonidae is also rejected in our analyses. The subfamily Palaemoninae is separated into three major clades corresponding to some extent to their different habitats, while some taxonomic characters might reflect this environmental transition. Re-examination and classification works of some palaemonoid genera are strongly recommended. Besides, further intensive studies on the Pontoniinae are essential before a comprehensive systematic relationship within Palaemonoidea could be demonstrated.

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